BOWER SYSTEM AND STRUCTURES OF THE GOLDEN BOWERBIRD, *PRIONODURA NEWTONIANA* (PTILONORHYNCHIDAE)

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We examined 60 Golden Bowerbird, *Prionodura newtoniana*, bower sites, involving a total of 98 main (decorated) bower structures during 1978-1997. Only one main bower structure was decorated actively at any bower site during any one season. Bower sites were traditional (n = 49) or rudimentary (n = 11). Traditional sites were dispersed spatially throughout suitable topography at an average of one per 4.2ha, and at a mean nearest neighbour distance of 151 ± 44m (n = 12). Eighty-four per cent of 25 traditional sites were regularly attended consecutively for 20 seasons. Rudimentary sites were located 78 ± 36m from traditional sites and were rarely active for more than two seasons. Traditional bowers consisted of a single (36%) or two (64%) towers when first found; 14 of the single tower bowers later became two tower structures. Each bower had a bower perch of woody vine, near-horizontal living sapling, fallen dead branch or tree root averaging 4.6 ± 6.5cm diameter. Where they abutted the bower perch, tower sticks were aligned tightly into a platform(s), upon which decorations, typically greyish-green lichen *Usnea* sp. and creamy-white seed pods of *Melicope broadbentiana*, were placed. Mean minimum age of a traditional bower was 9.6 ± 6.3 years (n = 48), at a mean of two per site over time. Six such bowers were attended for 20 seasons. Mean distance of a new traditional bower structure from the replaced one was 14.3 ± 12.7m. New main bower structures started as small single arboreal conical or maypole-shaped structures. It took two to three seasons for them to reach full size. Fourteen arboreal towers of main bowers subsequently became terrestrial, because sticks accumulated beneath them. Small arboreal and terrestrial subsidiary bower structures, built at a mean distance of 5.4 ± 4.2m from main bower structures, sometimes formed the bases for a new main one; suggesting a function of subsidiary structures. We conclude that while bower size and shape are not conservative in this bowerbird, the platform area(s) upon which decorations were placed, are conservative in being specifically located, better constructed and in being decorated. The significance of bower form and adult male plumage in the Golden Bowerbird are discussed. ☐ *Golden Bowerbird, Prionodura newtoniana, Ptilinorhynchidae, bower sites, structures, building, dispersion.*

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The Golden Bowerbird, *Prionodura newtoniana*, represents a distinctive monotypic genus endemic to the Atherton Region of the Australian Wet Tropics, tropical northeast Queensland, above 680 m asl (Blakers et al., 1984; Nix & Switzer, 1991). This species, the smallest bowerbird (25cm in length and averaging 75g), is strikingly sexually dimorphic. Adult-plumaged males are predominantly brilliant yellow on their underparts, brownish olive above with a small bright yellow crest on the central crown, and a larger yellow nape patch. Females and immature males are pale grey below and brownish olive above.

The Golden Bowerbird is one of 16, of the total 19, bowerbird species (Ptilonorhynchidae) that has a polygynous mating system, in which males are promiscuous and females build and attend nests alone. Males build a large stick bower (Fig. 1) of the 'maypole' type, as do the four gardener bowerbirds of the New Guinea genus *Amblyornis*. This is quite unlike the cleared 'court' of *Scenopoeetes*, the 'mat' of accumulated fern fronds' of *Archboldia*, or the stick or grass 'avenue' type bowers of *Ptilonorhynchus, Chlamydera* and *Sericulus* spp. (Marshall, 1954; Gilliard, 1969; Cooper & Forshaw, 1977; Borgia, 1986; Frith, 1989; Frith et al., 1994, 1996a,b; Frith & Frith, 1989, 1993, 1994, 1995; Donaghey, 1981, 1996). Bowers of most bowerbird species require rebuilding or major refurbishment within and between each display season, but maypole bowers of Golden Bowerbirds, and of some of the closely related gardener bowerbirds, persist year to year (Pruett-Jones & Pruett-Jones, 1982, 1983).

The Golden was the last bowerbird to be discovered in Australia. For its early history see

FIG. 1. A traditional twin tower bower and its adult male Golden Bowerbird owner. Note where tower sticks meet the bower perch (black in this picture) they are more skillfully placed and aligned, into a discrete 'platform', than are sticks of the rest of the structure. Decorations are placed on and adjacent to these 'platforms' and those seen here are beard lichen *Usnea* sp., seed pods of *Melicope broadbentiana* and the creamy white flowers of *Darlingia darlingiana* (one in bird's bill).

Chisholm & Chaffer (1956). Bowers were first described by Broadbent (in Campbell, 1900), Day (in North, 1904); Broadbent, 1902; North, 1909; Sharp (in North, 1914) and De Vis (in Mathews, 1926). Photographs of a bower appeared in Jackson (1909), but it was not until much later that more bowers were described (Bourke & Austin, 1947; Warham, 1962; Chisholm & Chaffer, 1956; Chaffer, 1958, Chisholm, 1957, 1963; Gilliard, 1969; Marshall, 1954). Bowers typically consist of two stick towers, which may or may not be of equal height, or a bulky and irregularly-shaped single massif of sticks with a bower perch protruding from one side. Structures vary considerably (Frith, 1989). Each tower is built upon and around a supporting central sapling(s) or tree. Twin tower bowers are up to 1m apart and are interconnected by a living or dead, arboreal or terrestrial, horizontal or near-horizontal, perch. Bower decorations are placed on the more neatly-aligned tower sticks adjacent to and on the bower perch. These include: greyish-green lichen *Usnea* sp., creamy-white seed pods of *Melicope broadbentiana*, and whitish flowers of several plant species (Chisholm & Chaffer, 1956; Chaffer, 1958; 1984; Warham, 1962, Frith & Frith, 2000a). Several other, smaller, stick subsidiary bower structures ('gunyahs' of Broadbent, in Campbell, 1900), are built close to the main (decorated) bower structure. Bower building/maintenance/decoration reaches a peak during the display season, from late August-December on the Paluma Range. Such activity declines during the heavier wet season rains of January and/or February, and when birds are moulting. Renewed, post-moult, activity commences in mid-March and April (Frith & Frith, 2000a,b).

FIG. 2. Dispersion of 41 traditional bower sites of male Golden Bowerbirds: 12 in study area 1, 10 in study area 2, and 19 in adjacent extralimital areas. Each 50ha study area measured 1 × 0.5km. Those numbered are the 25 traditional sites examined seasonally (S78-S97; see Table 4). Note: single lines show creek systems, double parallel lines represent the dirt road from Paluma Township (entering at bottom) to Paluma Dam (to north) with a side track through SA1; the dotted line shows a snig-track through SA2 forest.

Bowerbird studies are numerous, but few deal systematically with variation in bower/court structures/sizes (as opposed to bower decorations) or provide comparative measurements of them. Exceptions are those of Borgia (1985) for the Satin, Diamond (1987) for Vogelkop, *Amblyornis inornatus*, Lenz (1993) for Regent, *Sericulus chrysocephalus*, Frith & Frith (1994) for the Tooth-billed, *Scenopoeetes dentirostris*, Frith et al. (1996a) for Archbold's, *Archboldia papuensis*, and Frith et al. (1996b) for Great Bowerbirds, *Chlamydera nuchalis*. The present study, carried out during 1978-1997, provides the first detailed information on variation in the structure and size of bowers of Golden Bowerbirds. It includes information on bower site location and dispersion, bower site constancy, bower age and bower building. Data on male seasonal activities at bowers, including attendance levels, bower maintenance, vocalisations, displays, decoration theft, and home ranges are presented elsewhere (Frith & Frith, 2000a,b), as will be data on bower ownership, male survival and home ranges (Frith & Frith, unpubl. data).

METHODS

STUDY AREA. This study was performed in upland tropical rainforest, classified as simple notophyll vine forest (Tracey, 1982), at about 850m asl, 7km from Paluma Township on the Paluma Range, NE Queensland. The main 50ha study area (SA1, at 19°00'S, 146°10'E) measured 1 × 0.5km and was permanently gridded with metal stakes (see also Frith & Frith 1994, 1995). A narrow dirt road bisected the length of the broad main ridge line of SA1 (Figs 2, 3). To the north of this road was a broad flattish ridge 30-50m wide and 600m long; with a discrete hill from which a slope, dissected by gullies, fell steeply down to a perennial creek. To the south the ridge was flatter and wider (240m); interspersed with patches of *Calamus*-dominated undergrowth and a system of creeks, except at the western end where it rose to a ridge and another

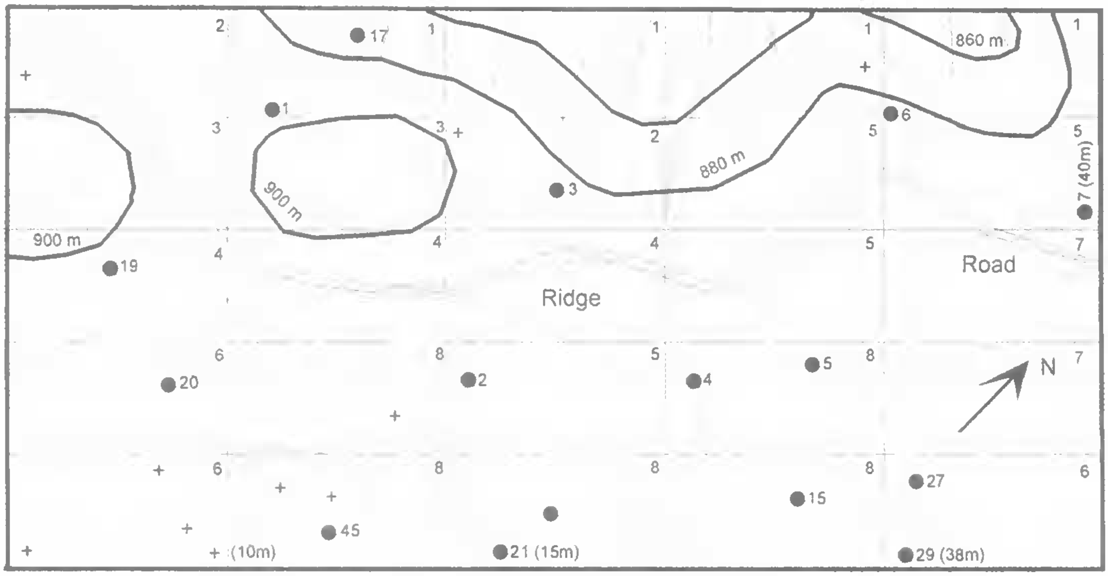

FIG. 3. Dispersion of 15 traditional (●) and 10 rudimentary (+) bower sites of male Golden Bowerbirds in study area 1 and outside (distance indicated in figure) its perimeter. Note: one rectangular quadrat = 2ha; number in top right hand corner of each = topographic type predominant (>75%) in that quadrat. Faint lines indicate location of seasonal gullies.

hill. Beyond this area the terrain dropped away steeply. A second hill-side study area (SA2) of the same size was not gridded. It was contiguous with SA1 and extended northwestwards up a hill to 950m asl. An old forestry snig-track bisecting a narrow ridge provided access up this hill (Fig. 2). Both study areas were searched systematically for bowers by CBF during August 1978-February 1981 for a total of 975h, besides innumerable unrecorded hours of random searching during the course of this and other bowerbird studies (Frith & Frith, 1994, 1995, 1998). Extralimital areas along tracks and ridges for a distance of up to 2km beyond SA1 and SA2 were also casually searched, as were other areas around Birthday Creek Falls and Paluma Dam.

DEFINITIONS. 'Site' describes the location of any active bower found, and any replacement bower(s) built subsequently during the course of the study. A traditional bower site was one attended for at least two seasons (Frith & Frith, 1994). A traditional bower was a large and well-established (single or twin tower) structure that was regularly attended, maintained, and decorated, throughout subsequent seasons by its traditional adult male owner. In a few instances, after the disappearance of a long-term traditional adult male owner, a traditional bower site was irregularly attended by immature (female-plumaged) males, who either maintained the existing traditional bower or built a new rudimentary structure at that site (Frith & Frith, 2000b). Such a rudimentary bower subsequently became larger, and a traditional one, once an adult male again attended the site regularly.

A rudimentary bower site was one established near a traditional site by the construction of a rudimentary bower. Such bowers were poorly constructed, maintained, decorated and irregularly attended for only a few days/weeks each season, by immature males. We use regularly attended to imply full-time seasonal attendance by traditional owners at traditional bowers, and 'irregularly attended' to imply part-time seasonal attendance by immature males at traditional or rudimentary bowers. We refer to a display season by the year in which it started (S78, S79 etc).

BOWER SITES, THEIR LOCATION AND DISPERSION. We located 60 bower sites and 98 main bower structures (Table 1). Each bower site was plotted and each bower numbered (site number followed by suffix a, b, etc., for every bower built at a site) and tagged with a scored aluminium label on a tree supporting a bower tower.

The possible influence of differing topography upon bower structure and dispersion of 12 traditional bower sites in SA1 was examined.

TABLE 1. Number of bower sites, bower types (traditional or rudimentary) and bower structure of male Golden Bowerbirds and the type of bower structure (single or twin tower) when first found on the Paluma Range, north Queensland. * = at least 14 became twin tower bowers during the study.

	Total number		Number of old bowers (before 1978)			Number of new bowers (1978-1997)		
	Sites	Bowers	Single tower	Twin towers	Total	Single tower *	Twin towers	Total
Traditional	49	86	1	11	12	30	44	74
Rudimentary	11	12	3	0	3	8	1	9
	60	98	4	11	15	38	45	83

Various quadrat grid sizes were uniformly applied to a topographic map of the study area to find the most suitable grid size that resulted in each quadrat containing >75% of a given topographic type (see Frith & Frith, 1995). This proved to be a grid of 25 quadrats each of 2ha, or 200 × 100m. Each quadrat was assigned to the topographic type predominating (Fig. 3) as follows: 1) very steep slopes of >40° dissected by gullies (8ha); 2) steep hill slopes of 20-40° (4ha); 3) hill tops with 10-20° slopes (4ha); 4) gentle hill slopes of 5-10° (6ha); 5) ridge-side with <10° slopes (8ha); 6) open flat or <5° sloping areas (6ha); 7) disturbed flat areas with dense understorey dominated by *Calamus* (4ha); 8) flattish to <5° sloping areas dominated by creek systems and dense understorey (10ha). To test whether dispersion of bower sites was random, the numbers of sites per quadrat was compared to expected Poisson distributions. Coefficients of dispersion (C.D: variance to mean ratio) were calculated as a quantitative description of dispersion. This method is based on the variance being equal to the mean in the Poisson distribution. Variance to mean values of 1.0 imply random, >1 implies clumped, and <1 implies a regular or spatially uniform distribution (Sokal and Rohlf, 1969). The significance level of an observed deviation of the C.D. from 1.0 was determined by a t-test (n-1, one-tailed), the t-value being calculated by dividing the difference between the C.D. and 1.0 by the standard error of the deviation.

Mean distances between traditional bowers at 12 traditional sites in SA1 and at three other sites just outside its perimeter (Fig. 3) were estimated in two ways. First, nearest neighbour distances (NND) between sites were analysed using the method of Clark & Evans (1954). In this method: when two sites are closer together than they are to any other ones then the same distance is included twice. Secondly, although bower sites were not arranged linearly in this area, we estimated the mean inter-bower distance. This involved taking the measurement from one bower to the next closest and so on throughout the whole 50ha. This allowed us to compare linear inter-bower distances with those presented in other bowerbird studies.

BOWER CHARACTERISTICS. Seventy-seven traditional bowers were measured and photographed. The following measurements were taken: height and base circumference of each tower and, in twin tower bowers, the distances between tower bases and apices; the type, axis direction, height and diameter of the bower perch and, in twin tower bowers, the length of perch exposed between the platforms of the towers; the number and girth at breast height (gabh) of saplings and trees incorporated into each tower. Number and size of associated arboreal and terrestrial subsidiary structures were measured and their distances relative to the main bower perch plotted. Means are given ± one standard deviation.

To give an indication of relative bower size we estimated bower volume by multiplying tower height with base circumference. Spearman rank correlation (one-tailed test corrected for ties) was applied to test whether there was a correlation between bower size (= volume) and situation (= degree of slope) at 42 traditional sites. When we measured two bowers at a site (n = 6) we took the mean value of each measurement.

BOWER SITE CONSTANCY, BOWER AGE, BOWER BUILDING AND STRUCTURAL CHANGES. To provide data on site constancy we examined 25 traditional bower sites from S78-S97 but excluding S91, S94 and S96 (Fig. 1). Our absences during these latter seasons did not affect our results as all sites save one (site 27) remained actively attended by birds during the subsequent season(s). We omitted season 91 because it was excessively dry, bowers were seldom attended and were poorly decorated. Rainfall typically averaged 259mm (S78-S90) for September-November; but in S91 only 94mm of rain fell, mostly after 12 November.

FIG. 4. Shapes and sizes of single tower bowers. (scales = a one metre stick marked every 10cm or CBF (180cm tall) or DWF (162cm tall) in picture). A, bower 37a: a compact single tower with a curved vine bower perch (right) with small terrestrial subsidiary (left in background). April 1979. B, bower 23a: a bulky single irregular-shaped massif with a sloping living-sapling bower perch (right). April 79. The few irregularly-placed sticks to the right end of the bower perch never became a second tower and the bower changed little in shape or size over six seasons. C, bower 22a: an amorphous three-peaked massif with a rotten bower perch on the ground (left of photograph). April 1979. The owner had replaced this bower with a new one by September 1979 (see Fig. 11C). D, bower 19a: an arboreal tower with a bower perch 161cm above ground. April 1979. The few irregularly-placed sticks to the right end of the bower perch subsequently became a second tower. E, bower 2a: a tall massif supported by a vine that also formed the bower perch 116cm above ground. April 79. It later became a twin tower structure.

The 25 traditional bower sites involved a total of 51 bowers. These bowers were described, photographed and/or measured during April 1979, August 1984 and February 1990; and in other seasons if their structure changed notably. Photographs were taken from the same location and height each time, so that temporal changes in bower shape and structure could be assessed accurately. These data provided us with information on age of bowers, changes to bower structure and bower building.

RESULTS

BOWER SITES, THEIR LOCATION AND DISPERSION. *Traditional Bower Sites.* We located 49 traditional bower sites (Table 1): 12 in SA1, 10 in SA2, 19 in adjacent extralimital areas (see Fig. 2), two near Birthday Creek Falls and six around Paluma Dam. Bower sites had medium to large forest trees, many saplings, and the odd tree ferns above and around them. Woody lianas and climbing pandans were common, but large stands of *Calamus* were not close to bowers. Canopy foliage cover was estimated above 37 sites: 12 having a coverage of >90%, 7 of 80-90%, 11 of 70-80%, five of 60-70% and 2 of 50-60%. Thus, 51% of sites had a cover of >80%, and 81% of >70%.

The direction of ground slope down and away from the bower was recorded for 45 bower sites: 20 were on a N to E bearing of 0-90°, 11 on E to S bearing of 100-175°, 2 on a S to W bearing of 210-240°, 8 on a W to N bearing of 280-360° and 4 were on flattish ground with no slope. The degree of slope on which bowers were placed at 45 sites were as follows: 17 on flat to 10° gentle slopes, 9 on 11-20° slopes, 6 on 21-30° slopes, 7 on 31-40° slopes and 6 on 41-45° slopes. Thus, bowers were built on slopes that averaged 21 ± 15°, with 71% being on slopes of <31°. On 0-10° slopes bower size (= volume; see Methods) averaged 740 ± 214cm^3, on 11-20° slopes 589 ± 208cm^3, 21-30° slopes 625 ± 223cm^3, 31-40° slopes 620 ± 240cm^3, and 41-45° slopes 684 ± 393cm^3. There was no significant correlation between bower size and degree of slope built upon (r_s = 0.22, P >0.05).

Bower sites were on flatter terrain and along ridge slopes either side of tracks or road, on gentle slopes and ridges immediately around the hill crest, and below steeper slopes where terrain levelled (Fig. 2). The 12 traditional sites in SA1 averaged one per 4.2ha, and were spatially dispersed throughout suitable topographic types (CD = 1.45, t = 1.54, P >0.1). Eight of the 12 were located on flat to gently sloping (<10°) ground (mean = one per 3.8ha) of topographical types 4, 5, 6 and 8 (Fig. 3). The remaining four sites (1, 3, 6 and 17) were located in topographical types 1 and 2 (one per 3.0ha), on steeper ground. No bower sites were found in topographic types 3 and 7.

In S78, the mean inter-bower linear distance from one site to the next closest one in SA1 (n = 12), and three additional sites (7, 21 and 29) just outside its perimeter (see Fig. 3), was 165 ± 41m (range 110-222m). Mean NND distance was 151 ± 44m (range 110-222m). During seasons S78-S90, the mean NND of bowers at these 15 sites varied from 138 ± 52 to 151 ± 47m (mean of mean = 147m). Differences were due to temporary disuse of bower site 20 during S87 and S88, and the establishment of replacement bowers at different locations within a site.

Rudimentary Bower Sites. We found 11 rudimentary bower sites (Table 1): ten in SA1 (including one just outside it; see Fig. 3) and another 140m outside SA1. Eight were on flat to gentle (<11°) slopes and the others on 21-30° slopes. Canopy cover was 70-85% (n = 3). Rudimentary sites in SA1 averaged 78 ± 36m (n = 8) from a traditional bower site. Of 11 rudimentary sites, three were attended for one season, one for two, and four non-consecutively for two, three (n = 2) and four seasons. Three others were abandoned when found (pre-S78).

BOWER CHARACTERISTICS. *Structure and Size of Traditional Bowers.* Traditional bowers were single or twin tower structures of sticks of varying lengths, texture and diameter (Fig. 1). Only one (the main) bower structure at any bower site was attended consistently, maintained and decorated during a season. We examined a total of 86 traditional bowers at 49 traditional sites: 12 were disused old bowers (11 being twin towered) that had been active before S78, but the other 74 were attended during some part of the study (Table 1). Of the 86 bowers, 36% had a single tower and 64% two towers when found. At least 14 single tower bowers subsequently became twin tower bowers (see Table 4), thus increasing the percentage of twin tower bowers to 80.

Single tower bowers varied greatly in shape and size from: a single compact conical structure with a curved vine bower perch (Fig. 4A); a single bulky, irregular-shaped large massif with a sloping living sapling bower perch (Fig. 4B); a huge amorphous multi-peaked massif with a base circumference 615cm and a rotten ground bower perch (Fig. 4C); an entirely arboreal structure with bower perch 161cm above ground (Fig. 4D); to a 205cm tall single massif with a 'liane' bower perch 116cm above ground (Fig. 4E). Single tower bowers had only one platform, even though a handful of sticks was placed at the opposite end of the bower perch in a few cases (see Fig. 4B,D)

FIG 5. Shapes and sizes of twin tower bowers. A, bower 29b: a bower with one tower terrestrial and the other arboreal. August 1984. Note: the sticks on the two bower perch platforms are conspicuously more neatly and tightly aligned. B, bower 4a: a bower with one terrestrial tower much larger than the other. April 1979. This bower changed little during the entire study. C, bower 20a: a 'classic' compact U-shaped terrestrial structure with two well-formed platforms. April 1979. Note: the sticks of the platforms meet on the bower perch and those of the towers have met and are fused beneath it. D, bower 17a: a bower with two widely-spaced but compact tall towers of similar height built on a large woody vine that also partly supported the tower on the right. April 1979. E, bower 10a: a bower with two widely-spaced amorphous towers. The vine bower perch also partly supports the tower on the right. April 1979. This bower changed little during the entire study (see Table 4). Note: it is easy to see how a bower like this may have originated from two low arboreal subsidiaries such as the ones in Fig. 8B. F, bower 16a: a skeletal bower with a rotten bower perch that, despite its appearance, was regularly attended from S78-S85 before being replaced by a new one. April 1979. The terrestrial subsidiary in the centre background rotted away.

at which site the second tower could be built to develop a twin tower structure.

A few either arboreal (Fig. 5A) or terrestrial (Fig. 5B) twin bowers had markedly

TABLE 2. Size (cm) and volume (cm^3) of single and twin tower traditional bowers of male Golden Bowerbirds on the Paluma Range, north Queensland. * = sample sizes vary because not all parameters of each bower were measured of each bower; ** = height (base to top apex) × base circumference.

	Single tower bowers			Twin tower bowers						Both towers		
				Larger tower			Smaller tower					
	Height	Base circum-ference	Volume **	Height	Base circum-ference	Volume **	Height	Base circum-ference	Volume **	Both towers volume ** com-bined	Distance between tower apices	Shortest distance between tower bases
Sample number *	15	13	13	60	39	39	60	39	39	39	34	38
Mean	148.6	439.0	646.6	130.3	347.1	456.6	82.8	209.5	197.0	654.0	98.4	24.6
s.d.	32.3	102.2	215	27.92	98.4	178.0	44.3	91.6	157.6	262.1	20.9	17.7
Range	100-205	274-615	320-1010	70-190	200-534	186-982	13-193	65-390	104-579	309-1449	70-150	0-80

asymmetrical towers. Eleven bowers had one larger terrestrial tower and a smaller arboreal one when first found. At least six arboreal towers subsequently became terrestrial due to an accumulation of dropped sticks beneath the structure. Typically, however, twin bowers had two well-formed towers with one tower taller and/or more massive than the other and their towers extending down to the ground. They varied greatly in shape and size: from a compact U-shaped structure (Fig. 5C) to widely-spaced neat (Fig. 5D), more amorphous (Fig. 5E), or skeletal (Fig. 5F) structures. The towers of the largest terrestrial bower were 174 and 198cm tall, with base circumferences of 5m and 3m respectively (Fig. 6A). In two bowers both towers were arboreal, with their bower perches 2m above ground (Fig. 6B).

Mean bower measurements for 15 single, and 60 twin, tower bowers are given in Table 2, where ranges exhibit the cumulative variation of bower structure outlined above. Single tower bowers averaged 13% taller, 21% larger around the base, and 29% bulkier (volume), than the larger tower of a twin bower. Moreover, their mean volume was similar to that of the mean combined volume of both towers of twin structures (= 654cm^3). In 55 twin bowers, the larger tower was both bulkier and taller than the smaller one, but in five bowers the bulkier tower was the same height (n = 3) or slightly shorter (n = 2; by 19 and 34cm). Distances between tower apices averaged 98 ± 21cm (n = 34), and between their bases 25 ± 18cm (n = 38). The bases of eight twin tower bowers were connected beneath the bower perch by the amalgamation of sticks of each tower (see Figs 5C, 10F).

Towers were built around, and supported by, saplings and vines (<25cm gabh) and/or trees (>25cm gabh). Larger single towers, and those of twin bowers, encompassed more such supports than did the smaller tower of a twin (Table 3). The gabh of saplings within bowers averaged 7.9 ± 5.7cm, and of trees 62.8 ± 23.6cm. Of 272 examined tower supports, 83% were saplings, 12% trees and 5% vines (12 woody vines and a *Calamus* vine). Four of the vines and two of the saplings also formed the bower perch.

The bower perch protruded from a single tower bower, or connected the two towers of a twin (see Figs 4-6). The axis of the bower perch was at right angles to the axis of the inter-tower bower 'avenue'. Bower perch compass alignment was recorded at 49 traditional bowers: 20 were aligned between 0-45°, 8 between 45-90°, 9 between 90-135° and 12 between 135-180°. The bower perch in 61 bowers consisted of: a woody vine (43%), living saplings leaning toward the horizontal (24%), a rotting dead branch or vine (24%) or a narrow tree root (3%; see Figs 4 & 5). Bower perches averaged 4.6 ± 6.5cm in diameter (Table 3). The top of bower perches averaged 42 ± 40cm (n = 59) above ground; but if the 4 atypically arboreal towers, with resultant unusually high perches, are excluded (see above) the average becomes 33 ± 19cm.

Where tower sticks met the bower perch they were conspicuously more neatly and tightly aligned into what we term a platform(s); see Fig. 1. Whereas single tower bowers had only one platform, twin structures had a platform at either end of the exposed bower perch. The mean length of exposed bower perch of twin tower bowers was 18 ± 8cm (n = 49), but the platforms of 4 such bowers actually met atop the bower perch

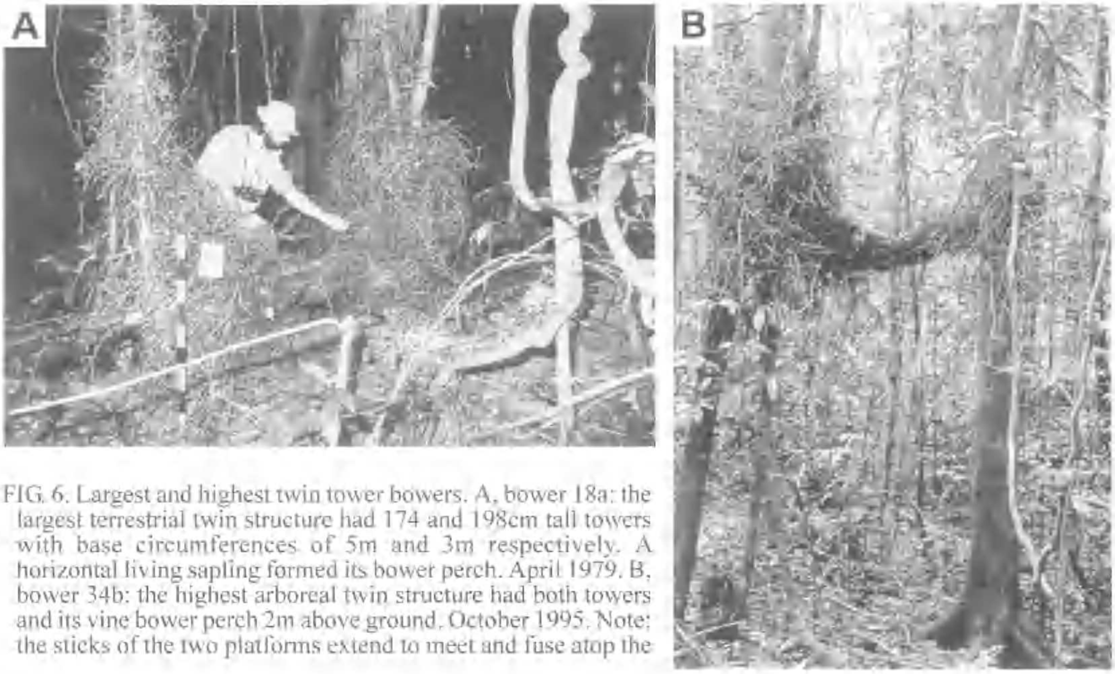

FIG. 6. Largest and highest twin tower bowers. A, bower 18a: the largest terrestrial twin structure had 174 and 198cm tall towers with base circumferences of 5m and 3m respectively. A horizontal living sapling formed its bower perch. April 1979. B, bower 34b: the highest arboreal twin structure had both towers and its vine bower perch 2m above ground. October 1995. Note: the sticks of the two platforms extend to meet and fuse atop the

(see Figs 5C & 6B). Bower decorations were placed only on platform sticks and those just beside/above them (Fig. 1). The relative quantities of each decoration type and their placement (i.e. on one or both platforms) varied from bower to bower and season to season. During peak display season, decorations consisted of a carpet (30-40 pieces) of greyish-green lichen *Usnea* sp. and 5-20 sprigs of creamy-white dehisced ripe fruit with attached black seed (seed pods hereafter) of melicope, *Melicope broadbentiana* (see Fig. 1). Other, less frequently used, decorations included creamy-white flowers of jasmine (*Jasminium kajewskii*), Brown Silky Oak (*Darlingia darlingiana*) and *Dendrobium* spp. orchids.

Structure and Size of Rudimentary Bowers. We examined 12 rudimentary bowers at 11 rudimentary sites (one site had two bowers built/attended during different seasons; see Table 1). These were poorly constructed, maintained, decorated and attended irregularly for only a few days/weeks each season, by immature males. They consisted of a conical-shaped loose mass of sticks lacking a platform, or with only an ill-defined one, and often lacking a bower perch or decorations (Fig. 7A). Height of their towers averaged 84 ± 12cm (n = 9; 3 being too old to measure), and mean volume 304 ± 188cm^3 (n = 3). Only one rudimentary bower had a second tower, a mere 50cm tall pile of sticks placed on the ground.

Following the disappearance of their long-term traditional adult male owners, a few traditional sites were irregularly attended by immature male(s) who built new rudimentary bower structures there. Rudimentary bowers at traditional sites were better formed, with a bower perch and more obvious platform (see Fig. 7B), than those built at rudimentary sites. They were all conical single towers (mean height = 95 ± 25cm, n = 5; mean volume 312 ± 102cm, n = 2). Some became a larger, and a traditional, bower once an adult male again regularly attended the site.

Structure and Size of Subsidiary Bower Structures. The frequent use, by males, of one or more favoured horizontal perches around bower sites resulted in birds placing, or leaving, sticks on them at the point they diverged from the trunk. Such sticks accumulated, became fused by fungi, and thus developed, over time, into subsidiary structures. Some subsidiaries were in the immediate vicinity of the main bower(s); (see Figs 4A, 5F), while others were up to 20m distant.

We recorded 36 terrestrial and 115 arboreal subsidiary structures at 46 traditional bowers; located at an average of 5.3 ± 4.2m from the main bower perch, and averaging 3.3 (range 1-16) in number per site (Table 3). All but four of the 46 bowers had several arboreal subsidiary structures (mean = 2.7, range = 1-13), but only 18

TABLE 3. Number and measurements (cm) of bower perches, tower supports and associated subsidiary bower structures at traditional bower sites of male Golden Bowerbirds on the Paluma Range, north Queensland. * = sample sizes vary because not all parameters of each bower were measured. ** = mean of means.

	Tower supports						Bower perches			
	Saplings/vines			Trees						
	Single tower bowers & larger tower of twin bowers	Smaller tower of twin bowers	Girth at breast height	Single tower bowers & larger tower of twin bowers	Smaller tower of twin bowers	Girth at breast height	Exposed length	Highest point (all bowers)	Highest point (excluding arboreal bowers)	Diameter
Sample number *	50	35	50	50	35	27	49	59	55	55
Mean	3.8	1.4	7.9 **	0.54	0.1	62.8 **	17.7	41.7	32.6	4.6
s.d.	2.6	1.3	5.7	0.7	0.4	23.6	8.1	39.3	18.8	6.5
Range	1-12	0-5	1-23	0-3	0-1	28.5-133	0-38	3-200	3-80	1.4-45

	Subsidiary bower structures					
	Terrestrial		Arboreal		Total number per bower site	Distance from bower perch
	Number	Height	Number	Height above ground		
Sample number *	18	18	42	42	46	46
Mean	2	68.6 **	2.7	168 **	3.3	532
s.d.	1	26	2.6	94.9	3.3	415
Range	1-5	15-106	1-13	36-388	1-16	0-2000

had terrestrial ones (mean = 2, range = 1-5). The height of arboreal subsidiaries, from their base to apex, averaged 168cm (range = 36-388cm) and that of the terrestrial ones 69cm (range = 15-106cm) from ground to apex.

Terrestrial subsidiary structures were built mostly around saplings, but a few incorporated a tree (Fig. 8A). Two subsidiaries were often built close together (<1m apart) on the same horizontal plane and resembled a miniature twin tower bower (Fig. 8B). A few subsidiary structures, particularly such pairs of them, subsequently became the basis for new main bowers. Arboreal subsidiaries were built where a branch forked horizontally from a sapling/tree trunk (Fig. 8C), or where a leaning sapling or vine crossed a sapling/tree trunk (Fig. 8D). Most (n = 90) were too high (>1.5m above ground at base) to measure. Those nearer the ground (<1.5m) were usually larger and conical, and averaged 61cm (range 20-120cm, n = 25) tall (Fig. 8D). As dropped sticks accumulated beneath them (n = 3), such arboreal structures became terrestrial ones. We recorded only one terrestrial and three arboreal subsidiaries at rudimentary bower sites.

Bower Site Constancy and Bower Age. Of the 25 traditional bower sites monitored seasonally (S78-S97), 84% were attended every season for 20 years (Fig. 2; Table 4). Of the 4 remaining sites: site 20 was attended for 18 (unattended S87-S88), site 27 also for 18 (unknown in S96, and derelict in S97), site 16 for 11, and site 21 for 5 (S78-S82) consecutive seasons.

Twin tower bowers were established and attended for the first 8 and 14 seasons at bower sites 20 and 27 respectively, but when their long-term adult male owners disappeared immature males took over and built and attended rudimentary bowers (2 at site 20 and 1 at 27, Table 4). Site 16 had 2 single tower traditional bowers attended consecutively by 2 adult males over 11 seasons (until S88) and was then abandoned (Table 4). There was only a rudimentary bower at site 21 in S78, but 14m away was a disused large twin tower flattened by a tree fall; it had obviously been attended during previous seasons. Its rudimentary bower did not change (S78-S82), was not replaced, and was only irregulary attended by one to several immature males before being abandoned.

The 25 traditional sites had a total of 51 bowers at them during the study (Table 4). Seven of these 25 sites had one main bower, 12 two bowers, 4 three and 2 four bowers; at a mean of 2 per bower site over time. Two bowers (15a and 20d) remained rudimentary for many seasons before becoming larger and traditional ones (see below), whereas three other rudimentary bowers (20c, 21a, 27b) did not progress and were abandoned (Table 4). Thus, of the 51 bowers, 48 were/became traditional and 3 remained rudimentary. The mean minimum 'life' of a traditional bower was 9.6 ± 6.3 (n = 48) years. Six traditional

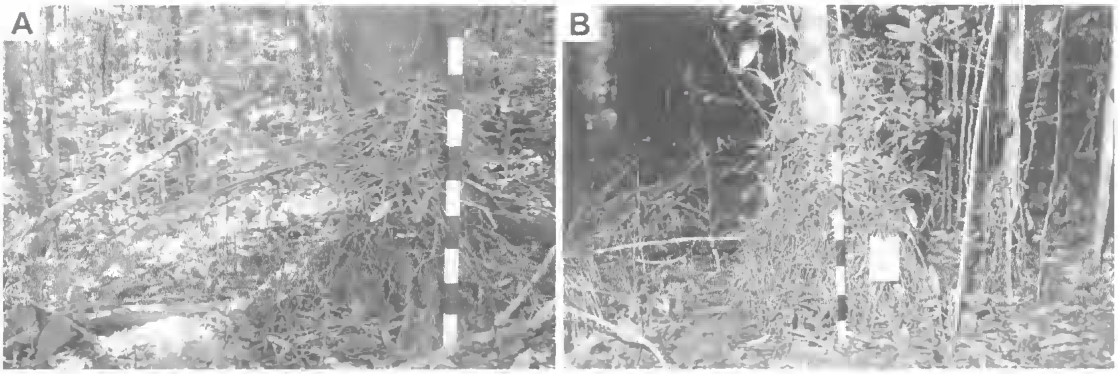

FIG. 7. Shapes and sizes of rudimentary bowers. A, this newly-built rudimentary bower (30) was first found at a new rudimentary site in August 1979. B, this rudimentary bower (21a) was built at a traditional site after a tree had destroyed the previous twin tower structure. It never increased in size and the site was eventaully abandoned.

bowers were attended for a minimum of 20 seasons (Table 4).

BOWER BUILDING AND STRUCTURAL CHANGES. We observed construction of 10 traditional bowers. Four (1a, 17b, 45b, 45c) started as completely new arboreal structures, 4 (3b, 6b, 20b, 47b) developed from an existing subsidiary bower structure, and 2 (15a, 20d) were built from existing rudimentary bowers, as follows:

In S78 we found only a derelict (pre-S78) bower at site 1. In March 1979 a handful of sticks had been newly-placed on a fallen horizontal sapling where it met a vertical tree, 20m distant from the derelict structure. This new bower (1a) resembled a sparse arboreal subsidiary, but it was decorated with two sprigs of melicope seed pods and one piece of lichen placed on *Freycinetia* sp. vine above the bower perch (Fig. 9A). By April 1980 the structure was a small conical arboreal subsidiary. By June 1980 it was an untidy tower of unfused sticks, lacking a platform and resembling a terrestrial rudimentary bower decorated with 10-12 lichen pieces (Fig. 9B, compare with Fig. 8A). By S80 it was a small terrestrial single tower, and by S81 a larger massif with a well-formed platform. Its bower perch subsequently slipped to the ground and a small handful of sticks placed on it 14cm from the large tower. By S82 this bower was a terrestrial twin, its second tower much the smaller (Table 4). It took 3.5 years to reach this stage.

Bower 17a was flattened by a tree fall in S85. In November 1986 we found a small conical arboreal bower (17b), of loosly-placed unfused sticks, where a leaning sapling crossed a vertical one, about 45m from the flattened bower and 63cm above ground. By October 1987 this was a terrestrial single tower, and a pile of sticks had been placed further along (20cm) the sapling where it crossed a large tree. By February 1990 the latter pile of sticks was a small second arboreal tower, and by November 1991 this was larger and terrestrial. It thus took four years for this bower to become a large twin tower structure (Table 4).

In December 1979 we found a newly-constructed small single conical arboreal tower of unfused sticks, piled between the vertical trunks of three saplings, 50cm above ground. This new bower (45b) was 20m from a derelict one of the previous season (Table 4). In S80 bower 45b was still small, but by S81 was a substantial terrestrial single tower bower that remained so until S88, but by which time it had deteriorated. In October 1989 replacement bower 45c, about 20m from 45b, was a single tall arboreal tower 60cm above ground. By September 1990 it was a twin tower bower with its second tower an arboreal one. By November 1991 both towers had become terrestrial (Table 4).

Four traditional bowers developed from an existing arboreal (6b and 47b) or terrestrial (3b and 20b) subsidiary bower (Fig. 9C,D). These took two to four years to become large single (47b) or twin (3b, 6b, 20b) tower structures (see Table 4). Traditional bower site 15 was attended only by immatures males from S78-S87, and its bower was small and rudimentary. When an adult male took over the site in S88 the rudimentary structure, unchanged for many years, became a larger single tower bower. By S90 it was a twin structure (see Table 4). Similarly, in S89 bower 20d was a new loosely-constructed rudimentary terrestrial tower attended by immature males. It

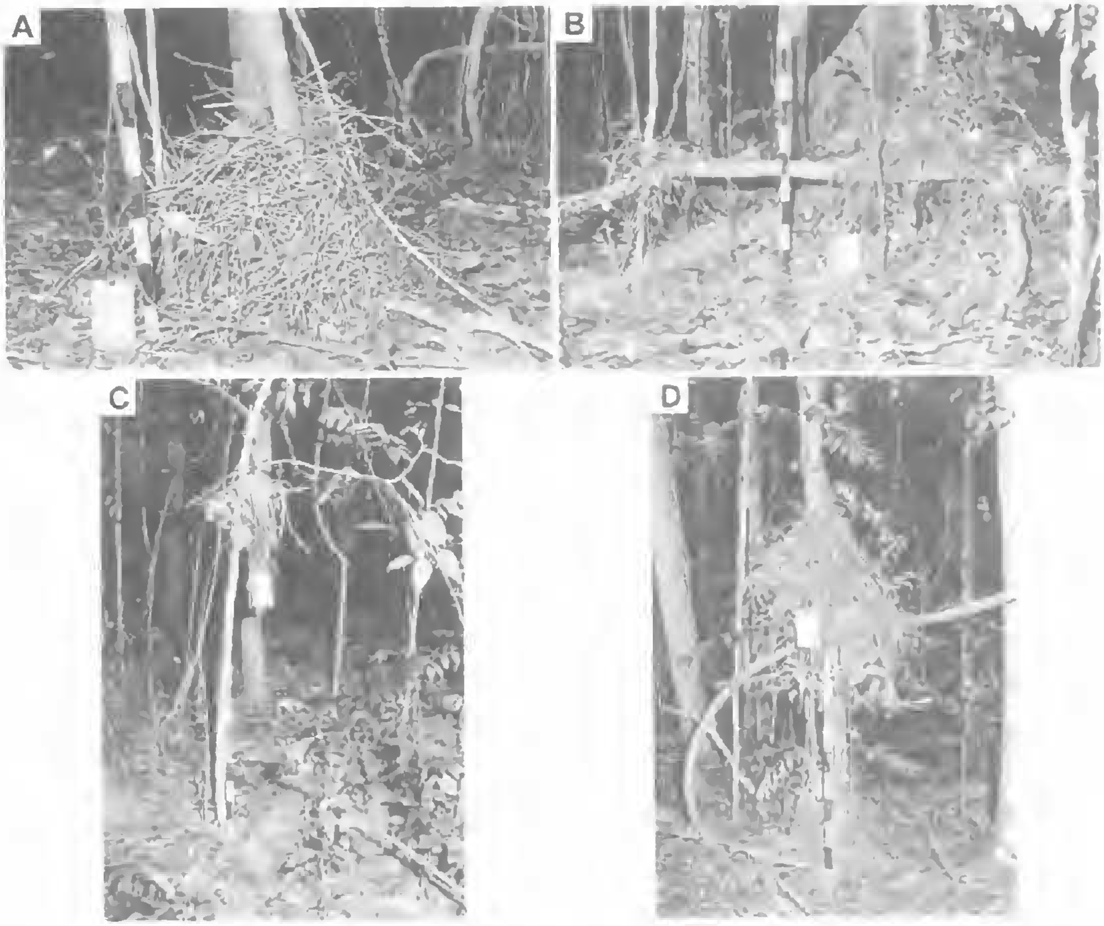

FIG. 8. Shapes and sizes of subsidiary bower structures. A, this terrestrial subsidiary was 4m from the main bower structure (20a) in April 1979. When bower 20a (see Fig. 5C) was damaged by a tree fall in January 1981, this terrestrial structure formed the basis of the new bower (20b). By S82 it was a twin tower bower. B, often two arboreal subsidiaries were built close together (<1 m apart) on the same horizontal support so that they resembled a miniature twin tower bower. April 1979. C, arboreal subsidiaries were usually built where a branch forked horizontally from the trunk of a sapling/tree. April 1979. D, this arboreal subsidiary was built where a vine crossed the trunk of a small tree. April 1979. Note: This subsidiary deteriorated but could have become an arboreal bower such as the one shown in Fig. 4D.

remained so until at least S93, but by S97 it was a substantial single tower bower (its ownership unconfirmed).

Numerous bowers progressed through stages of structural development similar to the above. Of the 48 traditional bowers examined at 25 traditional sites, 20 were initially single towers, but 14 of them were changed subsequently into twin structures (Table 4 and Fig. 10A-D). The original tower of these bowers remained the larger of the two. Moreover, the main towers of 8 arboreal (2 single and 6 twin) bowers subsequently became terrestrial ones, as did the smaller towers of 6 twin tower bowers (Table 4 and Fig. 10E,F).

Most second towers started as arboreal structures, because the bower perch was above ground. For example, bower 19a was an arboreal (128cm tall) single tower in S78, with but a handful of sticks at the far end of its bower perch (see Fig. 4D). Heavy rains in January 1981 caused the entire bower structure to slip toward the ground (bower perch from 161cm down to 60cm). In S82 it was an arboreal twin bower, the handful of sticks having been developed into the second tower, but both towers soon became

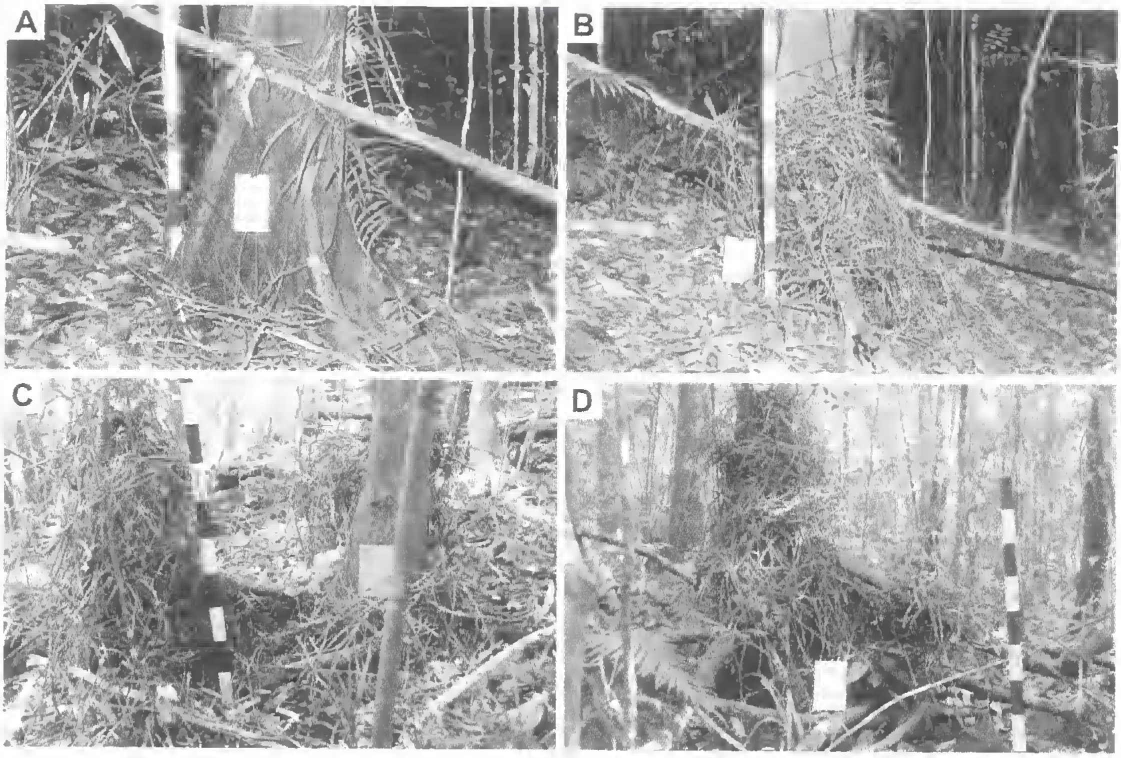

FIG. 9. Bower construction at traditional sites. A,B, bower 1a: this was little more than a handful of newly-placed sticks on a fallen horizontal sapling where it met a vertical tree in March 1979 (A) but by June 1980 (B) this had become a terrestrial tower of unfused sticks that lacked a platform. By September 1982 it was a twin tower structure. C, bower 6b: this originated in March 1980 from an arboreal subsidiary. The subsidiary formed the main tower and a second smaller tower was subsequently built at the opposite end of the bower perch about a small tree (right). This photograph was taken in August 1984, three and half years since building was commenced. D, bower 3b: this originated from a terrestrial bulky maypole-shaped subsidiary, May 1982. The subsidiary became the main tower and the handful of sticks on the right hand end of the bower perch later became the second tower/platform.

terrestrial, as dropped sticks accumulated beneath them. Similarly, bower 2a obviously started as an arboreal single tower, but sticks steadily accumulated beneath it until they reached its base and thus formed a huge single terrestrial massif (see Fig. 4E). It became even larger during subsequent seasons, but it was not until S90 that we noted the beginnings of a second tower at the opposite end of its bower perch (see Table 4).

The height of some single, and the larger of some twin, towers changed surprisingly little from season to season (Fig. 11A,B), whereas others increased in bulk as sticks were added (Figs 11C,D). Some reached the same or greater height (but not the bulk) of the larger tower (Table 4). After several seasons, some bowers deteriorated and became smaller as their towers decomposed or collapsed (Table 4). For example, in S78 bower 27a was a 'classic' twin tower structure with well-formed platforms (Fig. 11E). By February 1990 it had deteriorated, and its bower perch collapsed (Fig. 11F). It was replaced in S92, as were bowers 19a and 22b, after the extremely dry S91. Replacement was due to general bower deterioration, including the collapse of a main tower support and/or bower perch (n = 13), tree fall (n = 6) or mammal damage (n = 2). The mean distance of a replacement bower from the replaced one was 14.3 ± 12.7m.

We did not seasonally monitor subsidiary bower structures, but in August 1984 we did note that most of those recorded in S79 were deteriorating, or had disappeared, and new ones had replaced them at other locations about the main bower on the bower site.

DISCUSSION

We discuss our results in the light of previous Golden Bowerbird bower studies, and compare them mostly with data for the closely related rainforest-dwelling bowerbirds *Scenopoeetes*, *Archboldia* and *Amblyornis* spp. (see Kusmierski et al., 1993).

BOWER SITES, THEIR LOCATION AND DISPERSION. Traditional bower sites of Golden Bowerbirds were found on flattish to gently sloping ground along ridge flanks above steeper slopes, and mostly with >70% canopy cover above. None occurred on hill or ridge crests, or in disturbed forest dominated by *Calamus* palms and creek lines and their adjacent, typically steeper, slopes were avoided. Bowers have been described as occurring in similar sites on the Atherton Tableland (Day in North, 1904; Bourke & Austin, 1947; Chisholm & Chaffer, 1956; Chaffer, 1958; Warham, 1962; Gilliard, 1969; Crome & Moore, 1989; Frith & Frith, unpubl. data).

Bowers of the closely related gardener bowerbirds in New Guinea occur mostly on ridge crests or slopes below them (Simson, 1907; Rand in Mayr & Rand, 1937; Gilliard, 1969; Schodde & McKean, 1973; Diamond, 1972, 1987, 1982a). Pruett-Jones & Pruett-Jones (1982) examined 46 active bowers of Macgregor's Bowerbird, *Amblyornis macgregoriae*, on Mt Missim, Kuper Range and found 87% on ridge crests and the remainder 3-30m below crests on relatively level areas of the slope. They concluded that the habitat variables influenced the choice of bower site by Macgregor's Bowerbird rather than the selection of the ridge itself. They found such things as degree of canopy closure (>80%), slope and width of the ridge important factors for site selection. They found 42 bowers of Macgregor's Bowerbird spaced linearly and regularly along ridge crests at an inter-bower distance of 169 ± 64m. This figure is comparable with our Golden Bowerbird linear inter-bower measurement of 169 ± 40m, rather than our NND of 151 ± 44m (see RESULTS). Diamond (1987) estimated that distances between five Vogelkop Bowerbird, *Amblyornis inornatus*, bowers were several 100m. He pointed out that this was similar to the inter-bower spacing in Macgregor's Bowerbird and the 0.5km separation for eight bowers of the Golden-fronted Bowerbird, *A. flavifrons* (Diamond, 1982a).

Dispersion in Macgregor's Bowerbirds appears to be largely the result of socially interacting males utilizing available favoured topography. Its mating system has been characterized as being intermediate between lek behaviour and territoriality, with birds maintaining even dispersion in part by 'buffering their display space against intruder pressure' (Pruett-Jones & Pruett-Jones, 1982; pers. obs.). Traditional bower sites of the Golden Bowerbird averaged one per 4.2ha and were spatially dispersed, not clumped (contra Gilliard 1969: 321), throughout suitable topography. Male Golden Bowerbirds disperse their bower sites over suitable topography and habitat in an even way, similar to Macgregor's Bowerbird and apparently as a result of a similar social system. Dispersion of the bowers of Archbold's Bowerbird is also relatively even throughout suitable habitat (Frith et al., 1996a) and not clumped into leks (contra Diamond, 1982b).

Leks have been defined as requiring the following characteristics: clumped distribution of males; the ability of females to freely choose mates; no parental care by males; and no resources of value to females available at male display sites other than sperm (Bradbury, 1981). True lek behaviour has not been demonstrated in any bowerbird species (Donaghey, 1981; Pruett-Jones & Pruett-Jones, 1982; Diamond, 1986a; Borgia, 1986; Oakes, 1992; Lenz, 1993; Frith & Frith, 1995; Frith et al., 1996a,b, this study), as this requires that males at their bowers be in visual contact (Frith & Beehler, 1998). Rainforest-dwelling Tooth-billed Bowerbirds may be the only exception, as courts on the Paluma Range showed a dispersion intermediate between an even spread and true (i.e. exclusive) clumping (true lek) over suitable habitat (Frith & Frith, 1995). It remains to be demonstrated conclusively, that 'clumping' of male Tooth-bill courts does form a lek, albeit an exploded one. It is possible the dispersion of courts was the result of males utilising the only appropriate topography available, as appears to be the case in Golden and gardener bowerbirds.

Rudimentary bower sites and structures were short-lived, built and used sporadically by one or more immature males during one, several consecutive, or non-consecutive seasons. Similar rudimentary structures have been described for Macgregor's (Pruett-Jones & Pruett-Jones, 1982), Regent (Chaffer, 1984; Lenz, 1993), Satin (Vellenga, 1970; Donaghey, 1981; Borgia, 1986), Archbold's (Frith et al., 1996a), Great and Spotted (Frith & Frith, unpubl. data) Bowerbirds. Rudimentary bowers of *Amblyornis* spp., probably built by younger males, are often found at lower

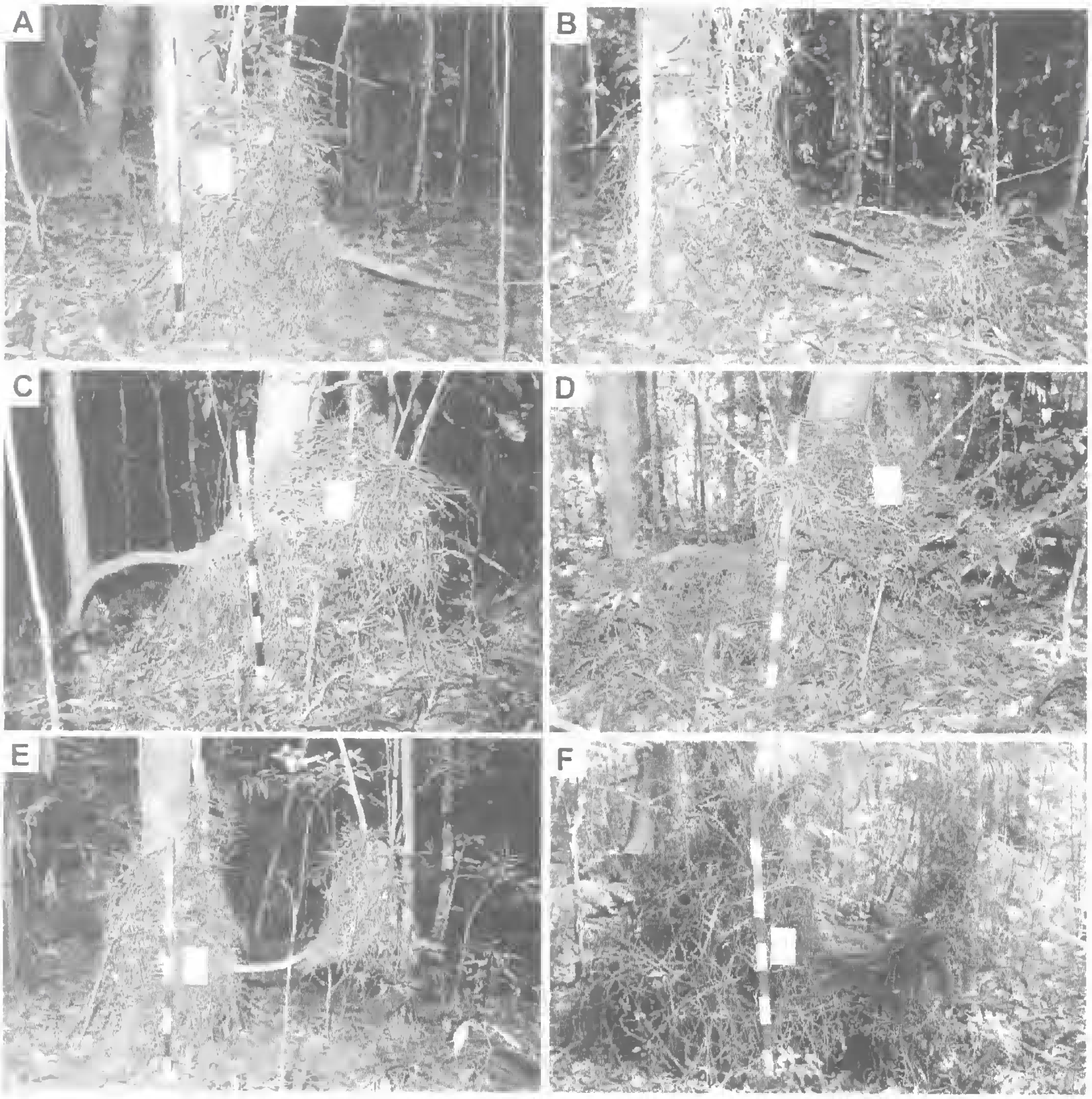

FIG. 10. Seasonal changes to the towers of traditional bowers. A, B, bower 34a: this was a single tower bower in April 1979 (A) but by August 1984 (B) was a twin tower structure with its main tower then 180cm tall. C,D, bower 8a: this was a single tower bower in April 1979 (C) but by February 1990 (D) was a massive twin tower structure. E,F, bower 33a: this had one of its towers small and arboreal in April 1979 (E) but by August 1984 (F) both towers were terrestrial. Note: sticks of both towers were fused beneath the bower perch.

altitudes than the traditional bower structures presumably built/owned by older males (Diamond, 1986b, 1987 and references therein).

BOWER CHARACTERISTICS. Previously the bower of the Golden Bowerbird was thought to consist only, or typically, of two towers, and with one tower usually taller than the other (De Vis in Meston, 1889; Campbell, 1900; Meston in Mathews, 1926; Cooper & Forshaw, 1977; Johnsgard, 1994; Schodde & Tideman, 1988; Donaghey, 1996). Our findings clearly show that bowers may be of one or two towers, and that their size and shape varies greatly (Table 4). In the case of traditional bowers, the structure of a single tower averaged some 20% larger than the average size of the larger tower of a twin structure. Moreover, its mean volume was similar to that of the mean combined volume of both towers of a twin structure. Thus, single tower bower structures may demonstrate to conspecifics that the owning male has expended similar effort in building as have males constructing a twin tower bower.

Golden Bowerbird bower perches or their 'avenues' did not exhibit a pattern of compass orientation, as is the case in several true avenue bower builders in which the avenue is aligned on or about the north-south axis (see Frith et al., 1996b). This orientation apparently enhances illumination of bower decorations and the displaying males (Marshall, 1954; Frith et al, 1996b). We did find that almost twice as many bower perches of Golden Bowerbirds were orientated to within 45° of the north-south axis, or the north-south half of the compass, than were to within 45° of east-west, or the east-west half of the compass rose. Thus, given bower perches were at right angles to the avenue between twin tower bowers, the orientation of the 'avenue' was predominantly within the east-west half of the compass. We can offer no explanation for these observations at present.

Sticks of Golden Bowerbird bowers, other than recently placed ones, become firmly fused together by the action of a fungus (Mathews, 1926; Chisholm & Chaffer 1956; Warham, 1962; Frith 1989, this study) ubiquitous to the lower forest sub-canopy (Jackson in Chisholm, 1957). Certainly, birds do not glue sticks together with saliva, or anything else, as suggested by some authors (e.g. Schodde, 1976; Diamond, 1987; Schodde & Tidemann, 1988).

Our long-term observations of rudimentary and traditional bowers indicated that most bower sticks are placed in a somewhat dishevelled fashion, resulting in great variation in bower shape and bulk. Their untidy construction suggests gross bower features are of less significance to females than is the discrete part of them modified into a 'platform(s)' for the exclusive placement of decorations. While traditional single or twin towered bowers varied greatly, they all had a conspicuous platform of more carefully and better aligned finer sticks to one end, or both ends, of the display perch. In view of bower structure quality in other bowerbirds (Borgia 1985, 1995; Borgia et al., 1985), it is possible that the quantity and quality of sticks/construction incorporated into the bower platform(s) is of significance to mate selection by females. Older and more dominant male Satin Bowerbirds that retain more bower decorations mate more often (Borgia 1985, 1995; Borgia et al., 1985). This suggests that bower platform(s) and their decoration represent characters of significance in female Golden Bowerbird mate selection. For a discussion and review of the significance of bower decoration, see Frith & Frith (2000a).

Broadbent (in Mathews, 1926) noted that larger main bowers of Golden Bowerbirds were surrounded by several 'gunyahs', dwarf-like hut structures, that we term subsidiary structures. Bulmer (in Gilliard, 1969: 305-6) reported similar subsidiary structures in Macgregor's Bowerbird. Of 151 subsidiary bower structures we recorded, 76% were arboreal and the remainder may have been originally arboreal. Often two such subsidiary structures, placed at an interval along the same length of horizontal branch, resembled a diminutive bower (Fig. 8B). Four such subsidiary structures had sticks added to them to subsequently replace, and become, the main bower.

It is possible that some subsidiary structures, around the main bower, at a traditional site are 'the casual products of social activity in non-breeding periods' (Chisholm & Chaffer, 1956: 13). Sharp (in Chisholm, 1929) claimed that only (adult) male Golden Bowerbirds attended large bowers and that subsidiary structures are built by females, but this is erroneous and may be a result of misidentification of female-plumaged, immature, males at such structures. It is our experience that these are initiated by the traditional bower owner, as a result of a bird leaving sticks at a favoured singing/perching perch(es). Adult males actively decorated only their single main bower structure, but would occasionally temporarily leave the odd decoration on a subsidiary one.

BOWER SITE CONSTANCY, BOWER AGE, BOWER BUILDING AND STRUCTURAL CHANGES. Most (84%) Golden Bowerbird bower sites were attended over 20 consecutive courtship seasons, predominantly by adult males (Table 4 and Frith & Frith, unpubl. data). Bower sites of Satins have persisted for up to 30 years (Vellenga, 1980), Spotteds for 13 years (Frith & Frith, unpubl. data), Greats for 13 years (Frith et al., 1996b), Tooth-bills for 20 years (Frith & Frith, 1995; unpubl. data) and Archbold's Bowerbird for 11 years (Frith et al., 1996a).

The mean minimum active 'life' of a Golden Bowerbird traditional bower structure was 9.6 ± 6.3 (n = 48) years. The main causes of structure replacement were deterioration due to age, the collapse of a tower(s) resulting from loss of supporting plants, or a falling tree directly

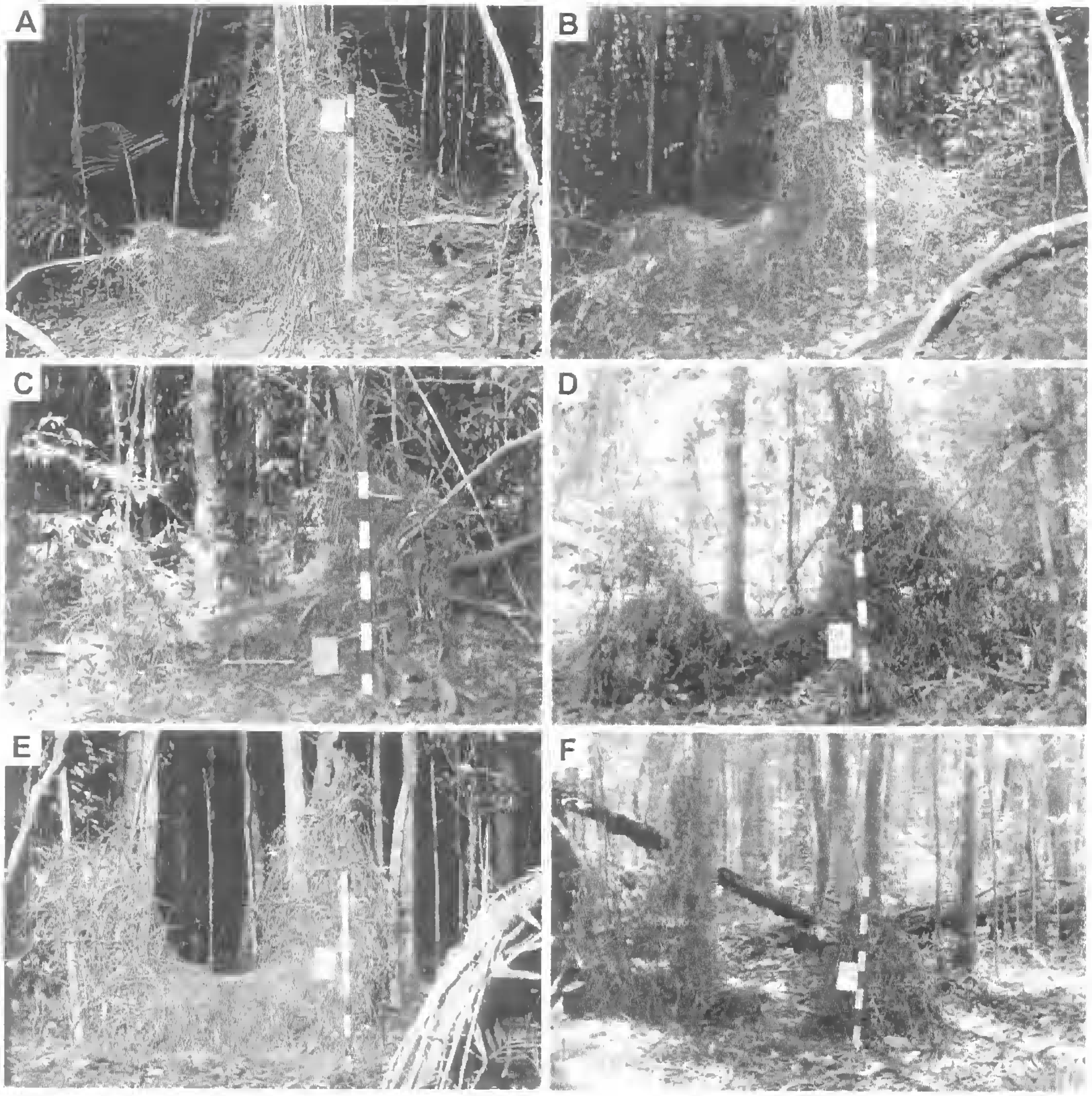

FIG. 11. Seasonal changes to the shape of traditional twin tower bowers. A,B, bower 3a: this changed little in size and shape between April 1979 (A) and February 1990 (B) despite the collapse of the dead trunk that was supporting the main tower. C,D, bower 22b: this changed little in overall shape from between September 1979 (C) and February 1990 (D), save becoming more massive. E,F, bower 27a: this changed dramatically in size and shape between April 1979 (E) and February 1990 (F), becoming smaller as its towers decomposed and collapsed.

damaging the bower and/or opening the canopy above the bower site. The larger traditional stick maypole bowers of *Amblyornis* spp. also persist year to year (Pruett-Jones & Pruett-Jones, 1982, 1983; pers. obs.). Conversely, bowers of the avenue-building *Chlamydera*, *Sericulus* and *Ptilonorhynchus* bowerbirds are refurbished and reused, or are replaced annually at the traditional bower site, but not always at the same location (Vellenga, 1980; Donaghey, 1981; Lenz, 1993, and references therein). Male Tooth-billed Bowerbirds annually re-create their court, more often than not in exactly the same place (Frith & Frith, 1994, 1995). Archbold's Bowerbirds typically renovate bowers at the beginning of each season (Frith et al., 1996a).

Earlier descriptions of Golden Bowerbird bower building were simplistic. For example, Day (in North, 1904) and Marshall (1954) noted that when a bower is first built it consists of sticks and twigs placed around two small trees growing about a metre apart. Each season sticks are added to the structures around two saplings until they are joined to form a U-shaped structure. In the centre, near the bottom of the U, a horizontal vine, stick or root is left bare (i.e. the bower perch). Our findings clearly demonstrate, however, that males in fact started each bower structure at a point above ground, where a leaning or horizontal branch (sapling, vine, fallen branch) crosses a vertical sapling or small tree trunk. New main bower structures started as small, single, arboreal, conical or maypole-shaped structures. They typically became fully terrestrial later, when dropped/fallen sticks accumulating on the forest floor reached their bases. Some bowers remained single tower bowers while others continued to grow into twin towers taking two to three seasons for them to reach full size.

Towers of some traditional bowers changed in shape and size from one season to the next, and often incorporated more saplings as they increased in size, whereas towers of others changed little from one season to the next. Dropped sticks may accumulate beneath the bower perch to there fuse to form a solid wall or 'a sort of hedge' (cf. Chisholm & Chaffer, 1956: 11); thus reinforcing the false impression of the structure originating on the ground. That most, if not all, Golden Bowerbird bowers originated above ground is a significant finding, given that all bowerbird species were thought to begin bower construction on the ground until Borgia & Sejkora (in Kusmierski et al., 1997: 310) stated that the Vogelkop Bowerbird builds its bower 'from the top down'. Thus the 'foundation' of the Golden (and Vogelkop?) Bowerbird's bower is not the clearing/cleaning of an area of ground (contra Stresemann 1953).

Diczbalis (1968) noted that male Macgregor's Bowerbirds start to clear a space around a young sapling, plucking off its leaves, bringing moss to form a basal ring around the sapling and 'trimming the space between base of sapling and the outside ring till it is clean and level. At the same time, the bird was bringing in its beak dry sticks and arranged these with its beak into spoke like shape around the sapling' to form a tower. He noted the structure was completed within a month, but would be improved and strengthened throughout the display season. Considering the arboreal beginnings of Golden Bowerbird bowers, clarification of bower development of the closely related *Amblyornis* species would be valuable. Were the original bowers of *Amblyornis* and *Archboldia* spp. arboreal, or has *Prionodura* 'raised' its point of initial bower construction from the terrestrial form of its ancestors?

SIGNIFICANCE OF BOWER FORM AND ADULT MALE PLUMAGE IN THE GOLDEN BOWERBIRD. The bowers, their decoration, the levels of attendance at them by males, and the plumage morphology and courtship displays of the Golden Bowerbird are of particular interest within the bowerbirds with regard to the 'transferral effect' postulated by Gilliard (1956, 1969). This theoretical effect suggests that, within several bowerbird genera, the degree of ornate/colourful plumage in adult males is inversely proportional to the complexity of their bowers. Thus, males of species developing more complex bowers, as external symbols of their dominance/fitness, have been able to replace their personal, and possibly costly (in making them conspicuous to predators), plumage ostentation with a bower structure and its decoration. The more impressive examples of this relationship occur within *Amblyornis* and the *Sericulus-Ptilonorhynchus-Chlamydera* clade. While the Golden Bowerbird is clearly most closely related to, and originated from ancestral, gardener bowerbird stock (Schodde, 1976; Sibley & Monroe, 1990; Kusmierski et al., 1993, 1997) it does not conform to the transferral effect discernible within these maypole builders. The maypole bower of the Golden has certainly lost some of the intricacies of *Amblyornis* bowers, in that it lacks a terrestrial moss base 'dish' (as in Macgregor's and Golden-fronted Bowerbirds) and its sticks do not form a 'hut' roof over a moss 'lawn' or 'court' (as in Streaked *A. subalaris* and Vogelkop Bowerbirds). Nevertheless it is a massive stick structure, with a discretely located platform(s), the construction of which is commenced above the ground. To what extent the arboreal point of initial bower construction is related to the significantly divergent adult male plumage in Golden Bowerbirds merits investigation.

Given its bower and, for present purposes, considering the Golden Bowerbird a member of *Amblyornis*, the transferral effect would lead one to predict a drab adult male plumage; at least no more colourfully ornamented than are the yellow- and orange-crested (but otherwise dully plumaged) simple maypole-building Golden-fronted and Macgregor's Bowerbirds. How then is the, apparently contradictory, massive maypole-bower building yet brilliantly-plumaged adult male Golden Bowerbird to be interpreted? Its colourful plumage is not dorsally confined to a crest, as in gardener and Archbold's Bowerbirds, but is also extensive on the nape and tail feathers. Moreover, the entire ventral surface of the bird is brilliantly colourful. This extensive colourful pigmentation of both dorsal and ventral plumage is, among bowerbirds, more reminiscent of adult male regent bowerbirds (*Sericulus* spp.). Adult male Regent Bowerbirds perch on exposed forest canopy branches, to advertise their bower location, and subsequently descend to the bower. During this initial advertisement, and descent, their bright plumage is doubtless conspicuous to females. Thus, we concur with Schodde's (1976) suggestion that, while bower-based courtship has apparently ornamented/coloured the dorsal plumage of more terrestrially-displaying adult male bowerbirds, the morphology of adult male Golden Bowerbirds, with bright underparts, reflects its elevated bower perch. It also reflects an extensive courtship flight display (Frith & Frith, 2000a). We view the bright central crown patch and the nape patch of the adult male Golden Bowerbird as homologous to the extensive crest of the gardener (especially *Amblyornis flavifrons* and *A. macgregoriae*) and Archbold's Bowerbirds. These characters, together with the brilliant yellow long forked tail, entire underparts, and pale iris lead us to concur with Kusmierski et al. (1993) in considering the Golden a highly ornamented bowerbird (contra Møller & Cuervo, 1998).

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TABLE 4. Continuity of 51 bower structures at 25 traditional bower sites of male Golden Bowerbirds on the Paluma. Range, north Queensland and structural changes over 20 consecutive seasons, from 1978-1997. * = AS = arboreal subsidiary; TS = terrestrial subsidiary; A = arboreal; T = terrestrial; NM = not measured; NC = no change; STB = single tower bower; TTB = twin tower bower; RB = rudimentary bower; ** = bowers found when under early construction.

Bower site and number	Number of seasons (=S) bower site attended	When examined	Main tower		Second tower		Status history *	Figure number
			Height (cm)	A or T *	Height (cm)	A or T *		
1a **	10 (S78-S87)	Mar 79	25	A			STB	9A
		Apr 80	NM	A			STB	
		June 80	75	T			STB	9B
		Sept 80	NM	T			STB	
		Sept 82	NM	T		T	TTB	
		Aug 84	110	T	48	T	TTB	
1b	10 (S88-S97)	Oct 88	NM	T			STB	
		Feb 90	141	T	13	T	TTB	
2a	20 (S78-S97)	Apr 79	205	T			STB	4E
		Aug 84	200	T			STB	
		Feb 90	198	T	10	A	STB	
		Oct 97	NM	T	15	A	TTB	
3a	14 (S78-S81, S84-S93)	Apr 79	148	T	47	T	TTB	11A
		Aug 84	NC	T	NC	T	TTB	
		Feb 90	170	T	57	T	TTB	11B
3b **	2 (S82-S83)	Apr 79	65	T			TS	
		May 82	133	T		A	STB	9D
		Sept 83	NM	T		A	TTB	
3c	4 (S94-S97)	Oct 95	NM	T		T	TTB	
4a	20 (S78-S97)	Apr 79	125	T	35	T	TTB	5B
		Aug 84	NC	T	NC	T	TTB	
		Feb 90	125	T	15	T	TTB	
		Oct 97	NM	T	45	T	TTB	
5a	20 (S78-S97)	Apr 79	184	T	30	T	TTB	
		Aug 84	NC	T	NC	T	TTB	
		Feb 90	140	T	20	T	TTB	

TABLE 4. *cont.*

Bower site and number	Number of seasons (=S) bower site attended	When examined	Main tower		Second tower		Status history *	Figure number
			Height (cm)	A or T *	Height (cm)	A or T *		
6a	2 (S78-S79)	Mar-79	93	T	75	T	TTB	
6b **	19 (S80-S97)	Mar-80	30	A			AS	
		Oct 80	NM	T	NM		STB	
		Sept 81	NM	T	NM	A	TTB	
		Aug 84	110	T	65	T	TTB	9C
		Feb 90	145	T	87	T	TTB	
7a	18 or 19 (S78-S95 or S96)	Apr 79	104	T	81	T	TTB	
		Aug 84	120	T	100	T	TTB	
		Feb 90	111	T	111	T	TTB	
7b	1 or 2 (S96 or S97)	Oct 97	NM	T	NM		STB	
8a	8 (S78-S85)	Apr 79	118	T			STB	10c
		Aug 84	NC	T			STB	
8b	3 (S86-S88)	Nov 86	NM	T			STB	
8a	9 (S89-S97)	Aug 89	NM	T		A	TTB	
		Feb 90	1070	T	55	T	TTB	10D
10a	20 (S78-S97)	Apr 79	122	T	83	T	TTB	5E
		Oct 85	NC	T	NC	T	TTB	
		Feb 90	114	T	88	T	TTB	
15a **	15 (S78-S92)	Apr 79	109	A			RB	
		Sept 84	NM	T			RB	
		Sept 88	NM	T	NM		STB	
		Feb 90	169	T	610	T	TTB	
15b	5(S93-S97)	Dec 93	30	T			STB	
		Oct 97	NM	T	20	T	TTB	
16a	8 (S78-S85)	Apr 79	150	T			STB	5F
		Aug 84	NC	T			STB	
16b	3 (S86-S88)	Nov 86	BM	T			STB	
17a	8 (S78-S85)	Apr 79	107	T	98	T	TTB	5D
		Aug 74	NC	T	NC	T	TTB	
17b **	12 (S86-S97)	Nov 86	NM	A			STB	
		Oct 87	NM	T			STB	
		Feb 90	168	T	121	A	TTB	
		Oct 97	NM	T	NM	T	TTB	
19a	14 (S78-S91)	Apr 79	128	A			STB	4D
		Oct 82	NM	A	NM	A	TTB	
		Aug 84	110	A	30	A	TTB	
		Nov 86	NM	T	NM	T	TTB	
		Feb 90	120	T	51	T	TTB	
19b	4 (S92-S97)	Nov 82	60	T	35	T	TTB	
		Oct 97	100	T	100	T	TTB	
20a	2 (S78-S79)	Feb 79	151	T	120	T	TTB	5C
20b **	6 (S80-S85)	Apr 79	66	T			TS	8A
		Jan 81	66	T	66		STB	
		Sept 82	NM	T	NM	T	TTB	
		Aug 84	110	T	110	T	TTB	
20c	1 (S87)	Oct 86	NM	T			RB	

TABLE 4. *cont.*

Bower site and number	Number of seasons (=S) bower site attended	When examined	Main tower		Second tower		Status history *	Figure number
			Height (cm)	A or T *	Height (cm)	A or T *		
20d	9 (S89-S97)	Jan 90	980	T			RB	
		Oct 97	125	T			STB	
21a	5 (S78-S82)	Apr 79	124	T			RB	7B
22a	1 (S78)	Apr 79	143	T			STB	4C
22b	13 (S79-S91)	Sept 79	110	T	95	T	TTB	11C
		Aug 84	170	T	130	T	TTB	
		Feb 90	174	T	95	T	TTB	11D
22c	6 (S92-S97)	Nov 92	NM	T	NM	T	TTB	
23a	9 (S78-S86)	Apr 79	128	T			STB	4B
		Aug 84	NC	T			STB	
23b	11 (S87-S97)	Oct 87	NM	T			STB	
		Oct 97	NM	T	15	A	TTB	
24a	5 (S78-S82)	Mar 79	112	T	111	T	TTB	
24b	6 (S83-S88)	Aug 84	125	T			STB	
24c	9 (S89-S97)	Feb 90	106	T	69	T	TTB	
26a	20 (S78-S97)	Sept 79	95	T	45	T	TTB	
		Aug 84	125	T	80	T	TTB	
		Feb 90	102	T	61	T	TTB	
27a	14 (S78-S91)	Apr 79	173	T	136	T	TTB	11E
		Aug 84	120	T	145	T	TTB	
		Feb 90	70	T	156	T	TTB	11F
27b	4 or 5 (S92-S95 or S96)	Nov 92	60	T			RB	
29a	5 (S78-S82)	Aug 79	120	T	30	T	TTB	
29b	15 (S83-S97)	Aug 84	140	T	35	A	TTB	5A
		Feb 90	140	T	101	A	TTB	
33a	20 (S78-S97)	Apr 79	130	T	128	A	TTB	10E
		Aug 84	160	T	140	T	TTB	10F
		Feb 90	141	T	155	T	TTB	
34a	16 (S78-S93)	Apr 79	100	T			STB	10A
		Aug 84	180	T	145	T	TTB	10B
		Feb 90	190	T	55	T	TTB	
34b	4 (S94-S97)	Oct 95	100	A	45	A	TTB	6B
45a	1(S78)	Dec 79	NM	T		T	TTB	
45b **	10 (S79-S88)	Dec 79	50	A			AS	
		Nov 80	NM	A			STB	
		Oct 81	NM	T			STB	
		Aug 84	120	T			STB	
45c **	7 or 8 (S89-S95 or S96)	Oct 89	125	A			STB	
		Sept 90	160	T	80	A	TTB	
		Nov 92	NM	T	NM	T	TTB	
45d	1 or 2 (S96 or SS97)	Oct 97	NM	T	NM	T	TTB	
47a	6 (S78-S83)	June 80	100	T	95	T	TTB	
47b **	2 (S84-S85)	June 80	38	A			AS	
		Nov 84	165	T			STB	
47c	12 (S86-S97)	Nov 86	NM	T			STB	